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Taxonomy of European Fannia larvae (Diptera, Fanniidae)

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With 20 Figures

I. Introduction

Fannia larvae are saprophagous and are commonly found in a great variety of habitats including fungi, decaying plant material and animal matter including excrement. The larvae of many species are found in the nests of birds, mammals and social Hymenoptera, and the larvae of a few species can occur inside the human body, causing myiasis (Chillcott, 1961: 34—35). Morphologically, the larvae of *Fannia* (and of the other genera of the family) are the best characterized larvae of the many families forming the group Schizophora. They possess a combination of apomorph characters which is unique in this large group of flies and which can be briefly summarized as follows: Body depressed and provided with a number of processes on all segments.

Hennig (1952: 386—87) listed all descriptions of *Fannia* larvae published up to that date, and based on these old and often incomplete descriptions the same author (Hennig, 1955: 12) presented a key to the larvae of eight European species, viz., *hamata* Macq., *canicularis* L., *fuscula* Fall., *manicata* Meig., *leucosticta* Meig., *incisurata* Zett., *scalaris* F. and *lineata* Stein. Only the larva of the last-mentioned species was new, but it was not described in detail. Furthermore this key did not separate the larvae of *fuscula* and *canicularis*, as this was impossible on the basis of the available descriptions.

The present author finds it impossible to accept the diagnosis of the larva of *Fannia hamata* Macq., originally presented by Séguy (1945: 154) and repeated without comment by Hennig (1955). The diagnosis of the *hamata* larva reads in the original as follows: „Stigmates postérieurs rapprochés, réunis sur une plaque commune; six paires de pseudopodes spinuleux sur la face sternale de l'abdomen". As will be seen after comparison with the following descriptions, and with all other descriptions of larvae of Fanniidae published to date, the two characters given for *hamata* involve so unique a deviation from the basic morphological scheme of *Fannia* larvae, that if they are accepted the species will have a most isolated position. The posterior spiracles are widely separated in all other species and nowhere show any tendency towards fusion, and only three pairs of ventral processes are present in all other known *Fannia* larvae. For these reasons the larva of *hamata* is not treated further in the taxonomic part below.

Two *Fannia* larvae originating from Iceland were briefly described and figured by NIELSEN, RINGDAHL & TUXEN (1954: 118—120), but they were only tentatively identified as no reared material was available. The first larva was treated as *?postica* Stein, the second as *?tuberculata* Zett.. During a study of a large material of Diptera from the Faroes the present author (LYNEBORG, 1968: 52—53) found numerous samples containing larvae identical with the one described from Iceland as *?postica*. It soon became evident that this identification was incorrect and that this very characteristic larva in fact represented the hitherto unknown larva of *F. mollissima* Hal. This species, together with a few others, was until recently placed in a separate genus *Coelomyia* Hal. (PONT, 1964). Both larvae are redescribed in the following account, partly on the basis of the original Icelandic material.

The paper of CHILLCOTT (1961) on the Nearctic Fanniidae was a great step towards a better taxonomic understanding of the larvae as well as of the adults. It presented descriptions of larvae or puparia of sixteen species of *Fannia* occurring in the Nearctic region. The descriptions were exact, but, as it now appears, not detailed enough to secure separation of the numerous species. The larvae of the following already known European *Fannia* species were redescribed in this paper: *incisurata* Zett., *scalaris* F., *manicata* Meig. and *canicularis* L., and one further one, *genualis* Stein, was described for the first time. CHILLCOTT also used the earlier descriptions of *fuscula* Fall., *?postica* Stein and *?tuberculata* Zett. without having access to new material.

The larva of *F. hirundinis* Ringd. was briefly described and figured by NUORTEVA et al. (1961: 200, fig. 2), but the published photographs are so poor, that they give no basis for a taxonomic treatment of the species.

In the following taxonomic part the larvae of eighteen European species of *Fannia* are described, all based on personal examination of larvae or puparia. The larvae of the following species are described for the first time: *coracina* Lw., *monilis* Hal., *vesparia* Meade, *aequilineata* Ringd., *clara* Coll., *vespertilionis* Ringd., *umbrosa* Stein and *armata* Meig., and redescriptions are given of *scalaris* F., *incisurata* Zett., *manicata* Meig., *fuscula* Fall., *leucosticta* Meig., *canicularis* L., *lineata* Stein, *?tuberculata* Zett., *genualis* Stein and *mollissima* Hal.. The main part of the material originates from the LUNDBECK collection of the Zoological Museum of Copenhagen, and was mainly collected many years ago by the skilful Danish entomologist J. P. KRYGER. Additional material was kindly lent me for study by Mr. Michael ACKLAND, Oxford, and Mr. Adrian C. PONT, London.

II. External morphology of *Fannia* larvae.

CHILLCOTT (1961) presented the most comprehensive morphological descriptions of larvae of Fanniidae hitherto published. He also arranged the Holarctic species of *Fannia* into eleven species groups, some of which were divided into subgroups. Later, PONT (1964: 759) rearranged the *serena* group. These arrangements were based mainly on imaginal characters, as larvae of several of the larger species groups were unknown. The descriptions in the following pages include descriptions of larvae representing two species groups and one subgroup of which no larvae were previously known, and moreover give more precise descriptions, especially of the ventral structures, than those previously published. It would thus seem logical to compile a comparative descriptive section giving information on the development

of the various structures in the species-groups of which larvae are now known, and to try to use the facts for further discussion of the phylogenetic value and relationships of the groups (see p. 10).

The eighteen species are distributed in the groups and subgroups as follows:

scalaris F.			
incisurata Zett.			
coracina Lw.	*scalaris* subgroup	*scalaris* group	New
manicata Meig.			
monilis Hal.			New
fuscula Fall.	*fuscula* subgroup		
vesparia Meade			New
leucosticta Meig.	*pusio* subgroup		
canicularis L.			
aequilineata Ringd.			New
clara Coll.	*canicularis* subgroup	*canicularis* group	New
vespertilionis Ringd.			New
lineata Stein	*glaucescens* subgroup		(New)
umbrosa Stein	*spathiophora* subgroup	*postica* group	New
armata Meig.		*hirticeps* group	New
?*tuberculata* Zett.			(New)
genualis Stein		*lugubrina* group	
mollissima Hal.	*mollissima* subgroup	*serena* group	(New)

The species marked "New" are described for the first time, those marked "(New)" have only been imperfectly described previously. Larvae of the *postica* and *hirticeps* groups and of the *mollissima* subgroup were not previously known.

There can be no doubt that the presence of six pairs of prominent structures on each segment belongs to the basic pattern of all *Fannia* larvae. Three pairs of these structures are placed on the dorsal surface and can be named laterodorsals, dorsolaterals, and dorsomedians. The laterodorsals are always the strongest of all the structures, including those on the ventral surface, and are placed on the laterodorsal edges of the segments. The dorsomedians are of very variable size in comparison with the laterodorsals, but are always stronger than the dorsolaterals or at least of the same strength as these. They are situated more or less close to the midline and are never absent, though often minute. The dorsolaterals are of more inconstant occurrence. They are normally present, either as more or less strong processes near the base of the laterodorsals or as groups of projections near the base of the laterodorsals. They can be developed as real processes well separated from the base of the laterodorsals but may also be absent, especially on the thoracic segments, though also on the abdominal segments. The three pairs of dorsal structures are normally of rather uniform development on segments 4—10, though gradually increasing in length towards the rear. Modifications occur both on the thoracic segments (segments 1—3) and on the terminal segment (see later).

The three pairs of ventral structures, lateroventrals, ventrolaterals, and ventromedians, are always less strongly developed than the corresponding dorsal processes of same segment. The lateroventrals are placed on the lateroventral edges of the segments and are always present. Ventrolaterals are also always present though

often only as minute prominences. The ventromedians are at most present as small button-like prominences: on segments 2—3 there is one pair near the anterior margin and on segments 4—10 there are two pairs near posterior margin, but often the ventromedians may be absent. More details are given below. Ridges with spinelike projections are present between the ventrolaterals of segments 5—10, and the anterior part of the segment is often separated from the rest of the segment by a transverse furrow.

Segment 1 has two anterior processes and lateral processes in some species groups. The terminal segment always has six marginal processes, normally of a similar nature to the laterodorsals. The posterior spiracles are on more or less long stalks and are placed either on or near the lateral margin or are well separated from lateral margin. The mouth hooks have not been examined in the present study.

The comparative morphology of the different parts of the larval body will be described in the text below for all species groups listed in the table above. In the *scalaris* and *canicularis* groups, where several very closely related larvae are known, not all specific differences will be mentioned.

A. Dorsal surface

a. Segments 4—10

The development of the three pairs of prominent dorsal structures is illustrated in the figures accompanying the following specific descriptions and showing the segments 9—11. The structure of segments 9—10 can be taken as being representative of all segments 4—10, but, as mentioned above, the structures are normally less strongly developed on the first of the abdominal segments.

In all larvae of the *scalaris* subgroup the laterodorsals are much more strongly developed than both dorsomedians and dorsolaterals and are provided with long, furcate projections. These are longest in *incisurata* and *scalaris* (Fig. 4), shorter in *coracina* (Fig. 5), *manicata* (Fig. 6) and *monilis* (Fig. 7). The dorsomedians are very small and button-like in *incisurata*, *manicata* and *monilis*, while they are longer in *coracina* and *scalaris*. The very short dorsomedians of *manicata* and *monilis* may be seen in relation to the very short posterior spiracular stalks. The dorsolaterals show a development in the five species which is parallel to the development of the dorsomedians, but only in *incisurata* are the dorsolaterals as long as in *scalaris*. The dorsolaterals are placed near to the base of the laterodorsal processes in all five species.

In the two members of the *fuscula* subgroup, *fuscula* (Fig. 8) and *vesparia* (Fig. 9), the laterodorsals are long but provided with much shorter projections than in the larvae of the *scalaris* subgroup. The dorsolaterals are very small (absent on segment 4) and placed near to the base of the laterodorsals, while the dorsomedian processes are much longer than in any larvae of the *scalaris* subgroup.

The larvae of the *canicularis* group show a greater variation in the formation of the dorsal processes. The larva of *leucosticta* (Fig. 10) is approximately intermediate between the *scalaris* and *fuscula* subgroups, as the reciprocal length of the processes is as in the *fuscula* subgroup while the provision with lateral projections is as in the *scalaris* subgroup. The larva of *canicularis* (Fig. 11) has laterodorsals and dorsomedians which are long and of almost equal length, while the dorsolaterals are very small and placed near to the base of the laterodorsals. The same

two pairs of processes are long in *clara* (Fig. 12), but the dorsolaterals are also well developed in this species and are well separated from the base of the laterodorsals. Finally, in *vespertilionis* (Fig. 14), there are three pairs of dorsal processes of nearly equal size, all long and provided with very minute projections only. The larva of *lineata* (Fig. 15) representing the *glaucescens* subgroup, has the laterodorsals developed as in *canicularis*, while the dorsomedians are much shorter and the dorsolaterals totally missing.

It is a character shared by the larvae of the last four groups (represented by *umbrosa* (Fig. 16), *armata* (Fig. 17), *?tuberculata* (Fig. 18), *genualis* (Fig. 19) and *mollissima* (Fig. 20)), that the dorsomedians are always very short. In *umbrosa* there is an additional row of small projections anterior to the base of the dorsomedians of segments 5—10. Such projections are not present in the other four species. The laterodorsals are large and provided with lateral projections in *umbrosa, armata, ?tuberculata* and *genualis*, while they are very small in *mollissima*. The dorsolaterals are represented by a few projections near the base of the laterodorsals in *umbrosa, ?tuberculata*, and *genualis*, while they are totally absent in *armata*. In *mollissima* the dorsolaterals have the character of real processes, though they are short. They are well separated from the laterodorsals.

b. Segments 1—3 (Thorax)

The development of the three pairs of dorsal processes shows modifications on segments 1—3 compared with the development on segments 4—10. These modifications are illustrated in Figs. 1 a—k.

The five species of the *scalaris* subgroup have the laterodorsals of segments 2—3 well developed, but there are differences in the length of the lateral projections as illustrated by Figs. 1 a—c. The development of the dorsomedians here corresponds to their development on segments 4—10 as described above, i. e., the dorsomedians are comparatively large in *scalaris* and *coracina* (Fig. 1 a), small in *incisurata, manicata* and *monilis* (Figs. 1 b—c). In all five species the dorsolaterals are developed as very small, button-like prominences near the anterior corners of the segments. Segment 1 has a pair of comparatively short anterior processes, and lateral processes are not present. Number of spiracular processes 7—9 in *scalaris, incisurata, coracina* and *manicata*, but only 2 in *monilis*.

The two species of the *fuscula* subgroup (Figs. 1 d—e) have long and narrow (i. e., with only very short lateral projections) laterodorsals, and the dorsomedians are also long. The very small dorsolaterals are present on segment 2 only and are well separated from the anterior corners. The anterior processes of segment 1 are rather long, and lateral processes are not present. Number of prothoracic spiracular processes 9—10.

The laterodorsals of segments 2—3 are long and slender in all species of the *canicularis* group (Figs. 1 f—h). In *canicularis* (Fig. 1 f) and *lineata* (Fig. 1 h) the dorsomedians are shorter than the length of a segment (as they are also in *leucosticta*, not figured), while in *vespertilionis* (Fig. 1 g) the dorsomedians are longer than the length of a segment. The development of the dorsolaterals shows much variation in this group. These processes are small and placed about mid-way between the dorsomedians and the laterodorsals (compare with the *scalaris* subgroup) in *leucosticta, canicularis* (Fig. 1 f) and *clara*. In *vespertilionis* (Fig. 1 g) they have the same position but are very long, while they are totally absent in *lineata* (Fig. 1 h).

Also the length of the anterior processes of segment 1 shows differences, as will be seen from the figures; lateral processes are absent in all species. Number of spiracular processes is normally 7—8, though only 3 in *lineata*.

It is a character shared by the species of the following four groups that they possess lateral processes on segment 1, though they are very short in *genualis* (Fig. 1 j). All species have long anterior processes on segment 1, and the number of spiracular processes is 4 in *umbrosa* and *armata*, 5 in *?tuberculata*, 7 in *genualis* and 12 in *mollissima*. The laterodorsals of segments 2—3 are well developed in all species except *mollissima* (Fig. 1 k), where they are very short. This feature corresponds to the development of the laterodorsals of segments 4—10. The dorsomedians and dorsolaterals on segments 2—3 are comparatively well developed in both *umbrosa* (Fig. 1 i) and *?tuberculata*. Both are placed near the anterior margin, and the dorsolaterals near the base of the laterodorsal processes. In *armata* (not figured) the dorsolaterals are found on segment 2 only, but they are longer than in *umbrosa* (Fig. 1 i). In *genualis* (Fig. 1 j) only the dorsomedians are developed, while in *mollissima* (Fig. 1 k) both dorsomedians and dorsolaterals can be seen, although in both species they are very minute prominences, which are well separated from the anterior margins of the segments.

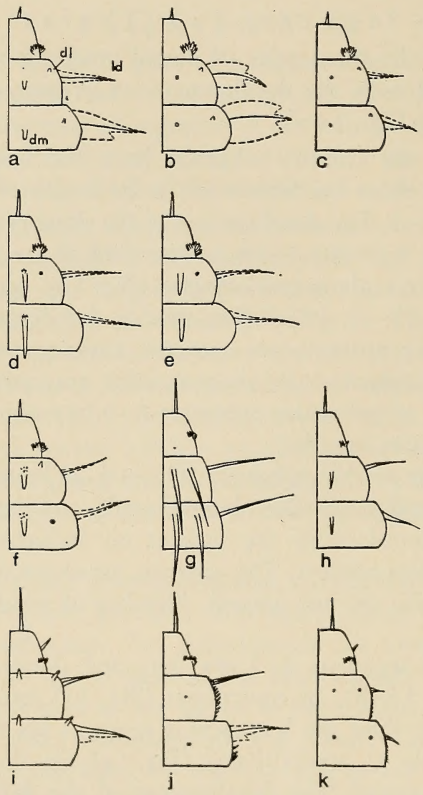


Fig. 1. Segments 1—3 in dorsal view of larvae of a. *Fannia scalaris* F., b. *F. incisurata* Zett., c. *F. manicata* Meig., d. *F. fuscula* Fall., e. *F. vesparia* Meade, f. *F. canicularis* L., g. *F. vespertilionis* Ringd., h. *F. lineata* Stein, i. *F. umbrosa* Stein, j. *F. genualis* Stein und k. *F. mollissima* Hal. The right parts of the segments and their prominent structures are shown in a schematical way. Abbreviations: dl = dorsolaterals, dm = dorsomedians, ld = laterodorsals.

c. Segment 11 (Terminal segment)

It can be stated that this segment always bears three pairs of marginal processes: a subapical pair, a sublateral pair and a lateral pair. The length of these processes and their armature of lateral projections corresponds closely with the shape of the laterodorsal processes of segments 9—10 in all five species of the *scalaris* subgroup. In the two species of the *fuscula* subgroup (Figs. 8—9) the same tendency occurs, though the sublateral pair is shorter than the other two pairs. This is also the case in the larvae of the *canicularis* group, the most distinct difference in size between the sublaterals and the other two pairs being found in *clara* (Fig. 12) and *lineata* (Fig. 15).

In *umbrosa* (Fig. 16) the lateral pair is strongest, the subapical pair much shorter and the sublateral pair a little shorter still. Also in *armata* (Fig. 17), *?tuberculata* (Fig. 18) and *genualis* (Fig. 19) the lateral pair is the longest and strongest, while the two other pairs are of almost equal size. Finally, in *mollissima* (Fig. 20) there are three equal pairs of short processes, each with a few long projections, and the entire lateral margin is provided with long projections. *Umbrosa* (Fig. 16) has an additional character, as a transverse row of short projections is present near the anterior margin.

The position of the posterior spiracular stalks seems to be of significant difference in the *scalaris* and *canicularis* groups on the one hand and the other four groups on the other hand. In the larvae of the first two groups the spiracular stalks are always placed on the dorsal surface at a good distance from the lateral margin. There is some variation in the length of the stalks. These are normally of considerable length in both groups, though they are very short and hardly raised above the surface in *manicata* and *monilis* of the *scalaris* group and rather short in *lineata* of the *canicularis* group. In the five species representing the *postica, hirticeps, lugubrina* and *serena* groups the posterior spiracular stalks are placed on or very near the margin anterior to the base of the lateral pair of processes.

The three spiracular processes are of rather equal size in the *scalaris* subgroup, rather short, radially arranged and more or less fused together. In the *fuscula* subgroup the same processes are all short and placed close together. In *leucosticta* (Fig. 10), representing the *pusio* subgroup, the median spiracular process is longer than the two lateral processes and is directed upwards and outwards. Approximately the same arrangement is found in *clara* (Fig. 12) of the *canicularis* subgroup. Other species of this subgroup, viz. *canicularis* (Fig. 11) and *vespertilionis* (Fig. 14), have the two most lateral spiracular processes placed close together, while the third process is directed inwards and backwards.

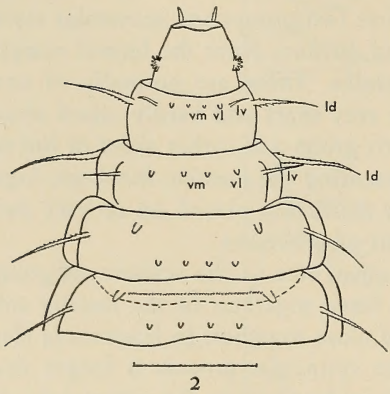
In the groups where the spiracular stalks are placed on or near the lateral margin, there is also some variation in the relative length and arrangement of the spiracular processes. In *umbrosa* (Fig. 16) the median process is very long and narrow, while the other two processes are very short and arranged around the base of the median process. The larva of *armata* (Fig. 17) has two long, posterior spiracular processes, of which one is directed upwards and the other outwards, and a short process anteroventrad to the base of the two long processes. The *?tuberculata* larva (Fig. 18) has three almost equal processes directed backwards. In *genualis* (Fig. 19) the posterior process is longest and the two other processes are placed above each other. Finally, the spiracular processes of *mollissima* (Fig. 20) are short, of equal size and arranged radially.

B. Ventral surface

a. Segments 1—3 (Thorax)

As mentioned earlier it is reasonable to accept three pairs of prominent ventral structures as belonging to the ground-plan of all *Fannia* larvae. Usually without exception the ventral structures are weaker than the corresponding dorsal structures on the same segment. Regarding segment 1 (prothorax) it can be stated that this segment never possesses ventral structures. It only has the two anterior processes and sometimes also lateral processes (see p. 5).

It was found that the development of the ventral structures of segments 2 and 3 in the *fuscula* subgroup was a good basis for a comparative description of these structures in all *Fannia* larvae. As will be seen, the *fuscula* larva (Fig. 2) possesses six ventral structures on a line near the anterior margins of segments 2 and 3 on approximatively the same level as the laterodorsals. The most lateral pair of these six processes is rather long, narrow and pointed, and represents the lateroventral processes. The four other structures are button-like prominences and represent the ventrolaterals and ventromedians. The *vesparia* larva shows the same arrangement, but the lateroventrals are shorter than in *fuscula*.



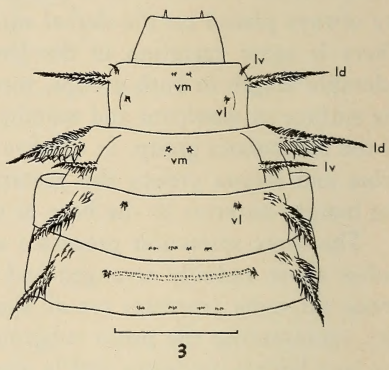


Fig. 2. Segments 1—5 in ventral view of larva of *Fannia fuscula* Fall. Scale: 1 mm. Abbreviations: ld = laterodorsals, lv = lateroventrals, vl = ventrolaterals, vm = ventromedians. The laterodorsals of segments 4—5 are omitted.

Fig. 3. Segments 1—5 in ventral view of larva of *Fannia scalaris* F. Scale: 1 mm. Abbreviations as in Fig. 2. The laterodorsals of segments 4—5 are omitted.

In the *scalaris* subgroup the same six ventral structures are present but in a somewhat different arrangement, as illustrated in Fig. 3 of *scalaris*. The short lateroventrals of segment 2 are situated antero-medially and close to the base of the laterodorsals, while those on segment 3 are much longer and are well separated from the laterodorsal processes. The ventrolaterals are represented by small prominences on segment 2, but are not present on segment 3. They have short projections and are situated mid-way between the anterior and posterior margins. The ventromedians are developed on both segments as a pair of small prominences near the anterior margin.

There is some variation in the development of the structures on segments 2—3 in other larvae of the *scalaris* subgroup. The ventrolaterals of segment 2 are much longer in *incisurata* than in *scalaris*, i. e., nearly half as long as the laterodorsals (!). On the other hand, in *manicata* and *monilis*, the ventrolaterals of segment 2 are developed only as groups of minute projections. There is also some variation in the length of the lateroventrals of segment 3, corresponding to the variations described below on segments 4—10. In all five species the ventrolaterals of segment 3 are missing. The ventromedian prominences in *incisurata* are represented on both segments 2 and 3 as in *scalaris*, but are missing in *coracina*, *manicata* and *monilis*.

The six larvae of the *canicularis* group show considerable variation in the formation of the ventral structures of segments 2 and 3, which are placed on a line as in the *fuscula* subgroup (Fig. 2). The lateroventrals are developed on both segments in all species; on segment 2 they are very short or button-like, while they are several times longer on segment 3. There is specific variation in their length corresponding to the variation of the same processes on segments 4—10 (see below). The ventrolaterals are developed as small prominences or as groups of minute projections on both segments in *leucosticta*, *canicularis*, *aequilineata* and *clara*. In *vespertilionis* the ventrolaterals are only developed on segment 3, where they are comparatively long processes, while they are absent on both segments in *lineata*.

The ventromedians are developed on segments 2—3 as small prominences or groups of minute projections in *leucosticta* and *clara*; on segment 3 only in *vespertilionis*; while they are absent on both segments in *canicularis*, *aequilineata* and *lineata*.

The larvae of *umbrosa*, *armata*, ?*tuberculata* and *genualis* all have lateroventral processes. They are short on segment 2, a little longer on segment 3, but always have the character of real processes. On a line between the lateroventrals there are two pairs of small prominences representing the ventromedians and ventrolaterals in *armata* and *genualis*, while in *umbrosa* and ?*tuberculata* the ventromedians are absent. The *mollissima* larva has six groups of short, spinelike projections representing the three ventral pairs of processes.

b. Segments 4—10

As a general rule the lateroventrals of segments 4—10 are always shorter than the laterodorsal processes of the same segment, though to a variable degree. Consequently there is also great variation in the size of these processes in the eighteen species under discussion. The ventrolaterals and ventromedians, if present, are with few exceptions developed only as small button-like prominences.

The *fuscula* larva (Fig. 2) has the lateroventrals of segments 4—10 developed as long, narrow processes. The ventrolaterals are short and rather thick processes, situated at the tips of the anterior ridge with minute projections on segments 5—10, while the ventromedians are developed as two pairs of small prominences near the posterior margin. The same arrangement is found in *vesparia* but both the lateroventrals and ventrolaterals are much shorter than in *fuscula*, the ventromedians are not developed though short, transverse ridges can be seen on segments 4—5 or 4—6.

In the species of the *scalaris* subgroup there is in general the same arrangement as in the *fuscula* subgroup, though with some variations. The lateroventrals are of about the same length as a segment and are provided with long projections in *scalaris* (Fig. 3) and *incisurata*, while in the other three species (*coracina*, *manicata*, *monilis*) they are from 1/4 to 3/4 of the length of a segment and are provided with

shorter projections. The ventrolaterals are small, button-like prominences in *scalaris, coracina, manicata* and *monilis,* while in *incisurata* they have the character of real processes, being half as long as a segment (!) and provided with projections. The ventromedians are developed as four small prominences near the posterior margin, but in *coracina* and *monilis* these prominences have the appearance of four groups of minute projections.

In the larvae of the *canicularis* group the lateroventrals of segments 4—10 are normally as long as or longer than the segmental length, and only in *lineata* are they two-fifths of the segmental length. They are provided with lateral projections as on the laterodorsal processes. In the *canicularis* group the ventrolaterals are developed as prominences or as processes shorter than one-fourth of the segmental length. In *vespertilionis* alone (Fig. 13) are they much longer and nearly equal to the segmental length. The ventrolateral prominences in *leucosticta* and *canicularis* are distinct, longer than wide at base; in *clara* still longer and provided with projections; and in *lineata* very minute. The ventromedians are normally present as four structures near the posterior margin in the larvae of the *canicularis* group, and only in *lineata* are they totally absent. They have the appearance of small button-like prominences in *leucosticta* and *canicularis,* as U-shaped projections in *vespertilionis* (Fig. 13), and as transverse rows of short, spinelike projections with a pair of furcate projections in *clara.*

Finally, in the five larvae representing the *postica, hirticeps, lugubrina* and *serena* groups the lateroventrals are much smaller than the laterodorsals of same segment. The length of the lateroventrals is one-sixth of the segmental length in *genualis* and about one-fourth of the segmental length in *umbrosa, armata* and *?tuberculata.* In *mollissima* they are still smaller, only appearing as small prominences. The ventrolaterals in these five larvae are developed as minute prominences, while the ventromedians are absent in *umbrosa* and *?tuberculata,* but developed as two widely separated prominences in *armata,* as four prominences in *genualis* and as four groups of minute spinelike projections in *mollissima.*

c. Segment 11 (Terminal segment)

Anterolaterad of the anal slit, the terminal segment bears a pair of prominent structures which are similar in nature to the ventrolateral structures of the preceeding segments, though often a little longer and stronger than the ventrolaterals of segment 10.

III. Larval morphology as evidence for the phylogenetic value and relationship of established species groups in *Fannia.*

It must at once be emphasized that in several of the largest species groups, such as the *postica, hirticeps, lugubrina* and *serena* groups, only a few species are known as larvae. We are, therefore, ignorant of the potential specific variation of the larval morphology within these groups. For these reasons the following remarks should be treated with caution, until more material is available.

A combination of two certainly apomorphic characters occurs in the known larvae of the four groups mentioned above, namely the presence of lateral processes on segment 1 and the position of the posterior spiracular stalks, these being „pressed out" towards the lateral margin and thus placed on or very near to the lateral

margin. These two characters are always combined with very small dorsomedian and dorsolateral structures, which is certainly a plesiomorphic condition. This should be assessed in relation to the habitats of these larvae, which live in media of a rather compact nature such as flood-refuse, sap on tree-trunks, under bark and stones, and in rotten wood. Such media certainly belong to the more original media of *Fannia larvae* (cf. HENNIG, 1965: 12).

However, it seems evident that this „out-pressing" of the posterior spiracular stalks is the result of convergent development. For instance, the exclusive Nearctic and Neotropical *benjamini* group, of which two larvae were described by CHILLCOTT (1961: 157, 159), also has the posterior spiracular stalks near the lateral margin, but the stalks are much longer and of a different nature than in the other four groups. Furthermore these two larvae do not possess lateral processes on segment 1.

In the larva of *mollissima* of the *serena* group the posterior spiracular processes are in somewhat different position from that in *umbrosa, armata, ?tuberculata* and *genualis*, and also the unique armature of long projections on the margin of the terminal segment seems to be a character of great importance. Unfortunately, only the *mollissima* larva is as yet known in the *mollissima* subgroup of the *serena* group. Of the other three subgroups of the *serena* group, only the larva of the North American *macalpinei* is known, belonging to the *sociella* subgroup. According to the description and figures of *macalpinei* given by CHILLCOTT, this larva is not closely related to the *mollissima* larva, but seems closely related to the *hirticeps* and *lugubrina* groups.

It would be ideal, although it seems too ideal, if the combined *postica, hirticeps, lugubrina*, and *serena* groups (perhaps with other inclusions) could be founded as a sister-group to the rest of the species groups in *Fannia*, this rest perhaps also including some of the other genera of the family, but our knowledge is still too limited to draw a final conclusion, especially as several groups are still unknown in the larval stage.

The majority of known *Fannia* larvae falls into the *scalaris* and *canicularis* groups. These larvae never possess lateral processes on segment 1, and the posterior spiracular stalks are in the apparently plesiomorphic position, more or less close to the midline. The three dorsal as well as the three ventral prominent structures show so many combinations of different developments and positions that it is a sheer guesswork to decide which conditions are plesiomorphic (primitive), pseudoplesiomorphic (reduced) and apomorphic (advanced, specialized), and to what degree convergence is involved. However, a few comments may be of value for future studies.

Firstly, it does not seem convincing to place the *scalaris* and *fuscula* subgroups as closely as was done by CHILLCOTT. The former subgroup has some characteristics which are certainly of apomorphic origin, such as the very long, furcate lateral projections on the laterodorsals, the irregular arrangement of the ventral structures of segments 2—3 (Fig. 3), and the presence of three equal terminal processes. The *fuscula* subgroup, on the other hand, has an apomorphic character in the very long dorsomedians, as is also found in all members of the *canicularis* group. The *fuscula* subgroup and the *canicularis* group both have, in opposition to the *scalaris* subgroup, short lateral projections on the laterodorsals, a regular arrangement of the ventral structures of segments 2—3 (Fig. 2), and the sublateral pair of terminal processes shorter than the two other pairs.

Secondly, regarding the *canicularis* group, the following information can be given. The only known representative of the *pusio* subgroup, *leucosticta*, shows affinity to both the *scalaris* subgroup and the *canicularis* subgroup, having apomorphic characters in common with both. The *glaucescens* subgroup represented by *lineata* seems to have a rather isolated position with such certainly reduced (pseudoplesiomorphic) characters as the loss of both dorsolateral and ventromedian structures on all segments. An apomorphic character is the shape and position of the sublateral terminal processes in this species.

The *canicularis* subgroup, on the other hand, seems to be an assemblage of species of diverse origin. The *canicularis* larva is certainly the most plesiomorphic in this subgroup, having only the dorsomedians and the laterodorsals well developed, while in *clara* and particularly in *vespertilionis* the dorsolaterals are also strongly developed and well separated from the laterodorsals.

IV. Key to larvae of eighteen European species of *Fannia*.

1 Posterior spiracles on dorsal surface of terminal segment well separated from lateral margin (Figs. 4—12, 14—15) . . . . . 2.
— Posterior spiracles near to or on lateral margin of terminal segment (Figs. 16—20) . . . . . 13.
2 Processes of terminal segment of equal size and normally provided with long, furcate lateral projections in about basal half (Figs. 4—7) . . . . . 3.
— Sublateral pair of processes of terminal segment distinctly shorter than both lateral and subapical pairs. Lateral projections normally shorter and more simple (Figs. 8—12, 14—15) . . . . . 7.
3 Dorsomedians represented by small button-like prominences (Figs. 6—7) . 4.
— Dorsomedians longer and with several projections (Figs. 4—5) . . . 6.
4 Dorsolaterals small and button-like, similar to the dorsomedians (Figs. 6—7). Posterior spiracles not on distinct stalks. Laterodorsals of segment 2 with short, lateral projections (Fig. 1 c). Ventrolaterals of segment 2 developed as short, button-like prominences (Fig. 3) . . . . . 5.
— Dorsolaterals much larger than dorsomedians, and provided with long, lateral projections. Posterior spiracles on distinct stalks. Laterodorsals of segment 2 with long, lateral projections (Fig. 1 b). Ventrolaterals of segment 2 long *incisurata* Zett.
5 Prothoracic spiracles with 7—8 processes. Anterior part of lateral processes of terminal segment with short projections (Fig. 6). Length of puparium 6.5 mm . . . . . *manicata* Meig.
— Prothoracic spiracles with 2 processes. Anterior part of lateral processes of terminal segment with long projections (Fig. 7). Length of puparium about 4 mm . . . . . *monilis* Hal.
6 Terminal processes with long, lateral projections on basal halfs or more (Fig. 4) . . . . . *scalaris* F.
— Terminal processes with shorter, lateral projections on less than basal halfs (Fig. 5) . . . . . *coracina* Lw.
7 Dorsomedians shorter than half length of corresponding segments. Dorsolaterals absent (Fig. 15) . . . . . *lineata* Stein

— Dorsomedians longer than half length of corresponding segments. Dorsolaterals present, at least on segments 4—10 (Figs. 8—12, 14) . . . . 8.
8 Dorsolaterals absent on segment 3 (Figs. 1 d, e) . . . . . 9.
— Dorsolaterals present on segment 3 (Figs. 1 f, g) . . . . . 10.
9 Dorsomedians distinctly shorter than laterodorsals, without long projections (Fig. 9) . . . . . *vesparia* Meade
— Dorsomedians not distinctly shorter than laterodorsals, with long projections (Fig. 8) . . . . . *fuscula* Fall.
10 Laterodorsals and terminal processes with long, furcate projections (Fig. 10) *leucosticta* Meig.
— Laterodorsals and terminal processes with short, simple projections (Figs. 11, 12, 14) . . . . . 11.
11 Dorsolaterals present as short projections near to base of laterodorsals (Fig. 11) . . . . . *canicularis* L. and *aequilineata* Ringd.
— Dorsolaterals longer and well separated from base of laterodorsals (Figs. 12, 14) . . . . . 12.
12 All three pairs of dorsal processes of almost equal size and with very short projections (Fig. 14) . . . . . *vespertilionis* Ringd.
— Dorsolaterals distinctly shorter than dorsomedians and laterodorsals, and all processes with longer but simple projections (Fig. 12) . . *clara* Coll.
13 Processes of terminal segment very short, not much longer than marginal projections (Fig. 20) . . . . . *mollissima* Hal.
— Processes of terminal segment much longer than the few marginal projections (Figs. 16—19) . . . . . 14.
14 Segment 2, and normally also segment 3, with dorsolaterals (Fig. 1 i) . . 15.
— Segments 2 and 3 without dorsolaterals (Fig. 1 j) . . *genualis* Stein
15 Row of short projections anterior to base of dorsomedians. Terminal segment with a transverse row of projections (Fig. 16) . . . *umbrosa* Stein
— No projections anterior to base of dorsomedians. Terminal segment without a transverse row of projections (Figs. 17—18) . . . . . 16.
16 Dorsolaterals present on segment 3. Laterodorsals of segment 2 without long projections at base . . . . . ?*tuberculata* Zett.
— Dorsolaterals not present on segment 3. Laterodorsals of segment 2 with long projections at base . . . . . *armata* Meig.

V. Descriptions.

Fannia scalaris Fabricius, 1794 (Figs. 1 a, 3, 4).

Material: Numerous larvae and puparia from a number of localities in Sweden, Denmark and Great Britain.

Description.

Dorsal view. Segment 1 with very short and slender anterior processes; on lateral margin a few short spinelike projections; no lateral processes. Prothoracic spiracles with 8—9 processes. Laterodorsals of segment 2—10 longer than length of corresponding segments. Laterodorsals of segment 2 provided with only a few long projections on posterior part near base. Laterodorsals of the following segments with long bifurcate or trifurcate projections for more than basal half. Projections of apical parts of same processes rather long and of gradually decreasing size. — Dorsolaterals of segments 2 and 3 developed as prominences with very short projections and situ-

ated near anterior and lateral margins. Same processes of the following segments situated medially to posterior part of laterodorsals; of about same length as basal projections of laterodorsals and provided with few bifurcate projections. — Dorsomedians of segments 2 and 3 short. Dorsomedians of the following segments a little longer than dorsolaterals and provided with some rather long, bifurcate projections. — Six processes of terminal segment of nearly equal size and provided with lateral projections as described for laterodorsals. — Posterior spiracles placed on moderately long stalks about half-way between lateral margin and midline. Spiracular processes short and nearly fused together. — Integument reticulate, dividing the surface up into small polygonal areas.

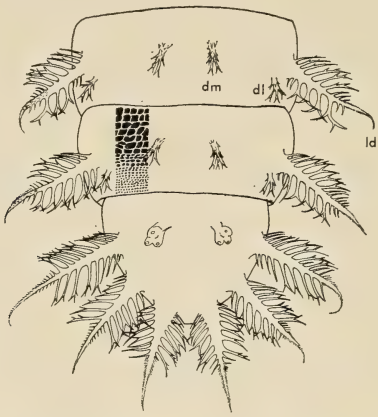


Fig. 4. Segments 9—11 in dorsal view of larva of *Fannia scalaris* F. Scale 1 mm. Abbreviations: dl = dorsolaterals, dm = dorsomedians, ld = laterodorsals.

Ventral view. Segment 2 with small lateroventrals situated antero-median to base of laterodorsals. Postero-median to, and further separated from, base of laterodorsals a pair of button-like prominences with short projections, which represent the ventrolaterals. At anterior margin of same segment a pair of minute prominences representing the ventromedians. Lateroventrals of segments 3—10 of about same length as corresponding segments and provided with projections distinctly shorter and more simple than projections of laterodorsals. Groups of spinelike projections antero-median to base of lateroventrals. — Ventrolaterals of segments 4—11 (not found on segment 3) button-like and provided with a number of short projections. Groups of spinelike projections laterally to ventrolaterals of terminal segment. — Ventromedians also present on segments 3—10, on segment 3 as a pair of small prominences near anterior margin (similar to position on segment 2), and on following segments as two pairs of small prominences near posterior margin of segments. Ventromedian prominences composed of several minute projections. Ridges with minute spinelike projections connect ventrolaterals of segments 5—10, but these segments not distinctly divided by transverse furrows.

Length of puparium: about 8 mm.

Fannia incisurata Zetterstedt, 1838 (Fig. 1 b).

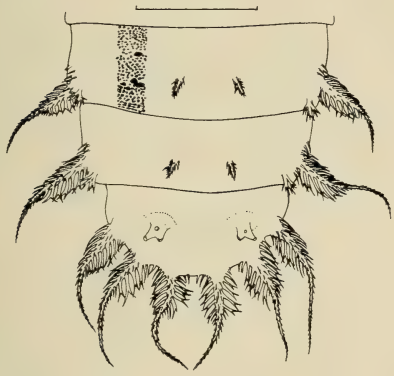
Material: 2 larvae without dates, (BM).

Description. Differs from the *scalaris* larva as follows:

Dorsal view. Laterodorsals of segment 2 with much longer and bifurcate pro-

jections, and basal projections of same processes on following segments also longer than in *scalaris* and often trifurcate instead of bifurcate. Dorsolaterals with more (about 8) bifurcate projections. Dorsomedians much smaller than in *scalaris*, developed only as button-like prominences (similar to *manicata*, Fig. 6).

Ventral view. Segment 2 with the same small lateroventrals antero-median to base of laterodorsals as in *scalaris* (Fig. 3). Postero-median to base of laterodorsals a pair of ventrolaterals much longer than in *scalaris*. Their length equals about half length of laterodorsals of segment 2. Lateroventrals of following segments with much longer bifurcate and trifurcate projections than in *scalaris*. Also ventrolaterals of segment 4—11 much longer than in *scalaris*; their length equals half length of a segment.



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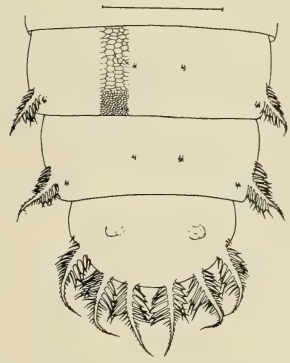

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Fig. 5. Segments 9—11 in dorsal view of larva of *Fannia coracina* Lw. Scale: 1 mm.
Fig. 6. Segments 9—11 in dorsal view of larva of *Fannia manicata* Meig. Scale: 1 mm.

Fannia coracina Loew, 1873. (Fig. 5).

Material: Denmark, Zealand, Lillerød, 26. IX. 1915, 17 larvae und puparia in nest of *Vespa vulgaris*, J. P. Kryger leg., ♂, ♀ reared 26. IV. 1916, Coll. Lundbeck, (ZMC).

Description. Very similar to the larva of *scalaris* (p. 13, figs. 1a, 3, 4), from which it can be separated by the following characters:

Dorsal view. Laterodorsals longer, with fewer and shorter projections restricted to basal third. Apical parts of these processes thus longer and with shorter projections than in *scalaris*. Dorsolaterals and dorsomedians shorter and with shorter projections than in *scalaris*.. — Six terminal processes also longer than in *scalaris*; their lateral projections restricted to basal fourth to third and shorter. — Posterior spiracles on shorter stalks.

Ventral view. As described for *scalaris*, but segment 2 without ventromedians and all other processes and prominences shorter.

Fannia manicata Meigen, 1826. (Figs. 1 c, 6).

Material:

Denmark, Zealand, Springforbi, 1 larva in decaying garden refuse, 17. III. 1960, Leif Lyneborg leg., (ZMC).

Great Britain, Durham, Corbridge, 1 puparium attached to male bred from garden refuse, March 1948, G. C. Varley, (Oxf. Mus.).

Great Britain, Durham, Newcastle, 1 puparium attached 2 males and 1 female bred from vegetable refuse, 16. IX. 1946, G. C. Varley (Oxf. Mus.).

Great Britain, Oxford, Headington, larva 24. III. 1917 in garden, em. 9. IV. 1917, A. H. Hamm, (Oxf. Mus.).

Description.

Dorsal view. Segment 1 with rather long and slender, anterior processes; no lateral processes. Prothoracic spiracles with 7—8 rather long processes. — Laterodorsals of segments 2, 3 and 10 about two-thirds of length of corresponding segments; those of segment 4—9 about half as long as corresponding segments. Laterodorsals of segment 2 with very short projections and those of the following segments with rather few and not very long projections in about basal half. Projections of posterior parts of these processes often bifurcate. Apical parts of laterodorsals comparatively short and with short projections. — Dorsolaterals represented on segments 2—10 as very small prominences with few short projections. Their position as described for *scalaris* (p. 13). — Dorsomedians represented by similar small prominences as dorsolaterals. — Six terminal processes of equal size and more compactly arranged than in the related species, i. e., with more open space between anterior margin of terminal segment and lateral processes. Terminal processes with rather long and often bifurcate projections in basal halves and very short projections in apical halves. — Posterior spiracles on very short stalks scarcely raised above surface. Spiracular processes placed on common rounded plates. — Integument with reticulate pattern.

Ventral view. Segment 2 with short button-like lateroventrals antero-median to laterodorsals (as in fig. 3). Small prominences which are composed of groups of projections situated postero-median to, and further separated from, laterodorsals represent the ventrolaterals. No ventromedians on segment 2 (as in fig. 3). — Lateroventrals of segment 3—10 about one-fourth as long as length of corresponding segments and provided with numerous simple and short projections. — Ventrolaterals not developed on segment 3, but present as button-like prominences on segments 4—11. Ventromedians very small and only represented by groups of minute projections. There are two groups near anterior margin of segment 3, and four groups near posterior margins of segments 4—10 (most lateral groups are often very indistinct). — Ridges between ventrolateral prominences not very distinct, and segments not divided by transverse furrows.

Length of puparium: about 6 mm.

Fannia monilis Haliday, 1838. (Fig. 7).

Material: Great Britain, Wimbledon Common, WATERHOUSE, 1 puparium. The larva was found in rotten bracken, ♂ emerged 20. IV. 1893, (BM).

Description. Very similar to *manicata* Meig. which is described above. The following differences can be given:

Dorsal view. Segment 1 without anterior processes in the single specimen available; no lateral processes. Prothoracic spiracles with apparently only 2 long processes. — Laterodorsals comparatively longer, and lateral margins of segments in front of laterodorsals provided with more spinelike projections than in *manicata*. — Terminal processes as in *manicata*, but lateral pair closer to anterior margin of terminal segment and anterior projections longer and continuing along lateral margins.

Ventral view. Practically as in *manicata*.

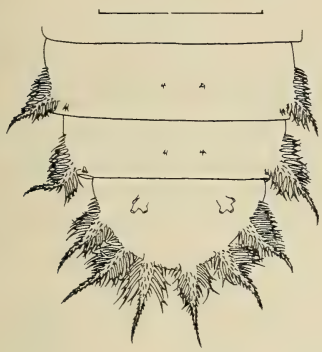
Length of puparium: 4 mm.

Fannia fuscula Fallén, 1825. (Figs. 1 d, 2, 8).

Material: Denmark, Zealand, Tibirke Mose, 29 larvae and puparia collected 12. X. 1921 in nest of *Bombus*, J. P. KRYGER leg., 4 ♂♂, 2 ♀♀ reared 30. V. to 12. VI. 1922, Coll. LUNDBECK, (ZMC).

Description.

Dorsal view. Segment 1 with rather long and slender, anterior processes; no lateral processes. Prothoracic spiracles with 10 short processes. — Segments 2—10 with long laterodorsals which increase in length and strength towards the rear and are at least as long as the corresponding segments. Laterodorsals of segments 2 and 3 with only short lateral projections; on the following segments with moderately



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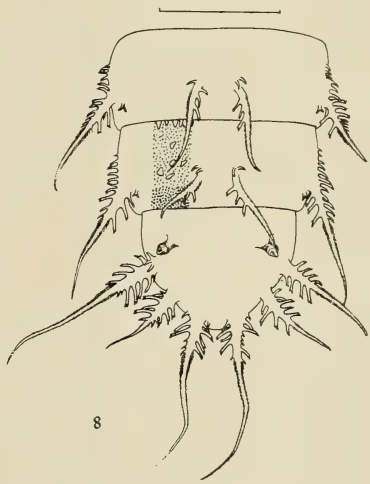

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Fig. 7. Segments 9—11 in dorsal view of larva of *Fannia monilis* Hal. Scale: 1 mm.

Fig. 8. Segments 9—11 in dorsal view of larva of *Fannia fuscula* Fall. Scale: 1 mm.

long, bifurcate, lateral projections in about basal third. Apical part of laterodorsals long, slender and provided with very short projections. — Dorsolaterals practically absent, only represented by small prominences on segment 2 and by very small, bifurcate projections at the base of laterodorsals of segments 5—10. — Segments 2—10 with long dorsomedians, similar in size to laterodorsals. Few short projections anterior to base of dorsomedians. — Terminal segment with subapical processes longest. Sublateral pair much shorter and lateral pair about as long as subapical pair. All terminal processes have long, lateral projections at base; apical parts long and with very short projections. — Posterior spiracles on distinct stalks half-way between midline and lateral margin. Spiracular processes all short and close together. — Integument densely granulated with larger „islands".

Ventral view. Segments 5—10 divided into two parts by transverse furrows curving up to anterior margin. Segments 2—10 with lateroventrals which are short on segments 2 and 3, longer and stronger on following segments, though always weaker than laterodorsals of same segment. They have very short projections. Segments 2 and 3 each with two pairs of small, button-like prominences on a line between lateroventrals. Lateral pair of these prominences represents the ventrolaterals, median pair the ventromedians. Ventrolaterals longer and stronger on segment 4—11 and placed on anterior part of each segment. Long ridges with close-set, very short, blunt spines between ventrolaterals, except on segment 4. — Ventromedians of

segments 4—10 represented by four button-like prominences on median, posterior part of each segment.

Length of puparium: about 7 mm.

Fannia vesparia Meade, 1891. (Figs. 1 e, 9).

Material: Denmark, Zealand, Ruderhegn, 1 larva and 1 puparium collected in September 1913 in nest of *Vespa germanica*, J. P. KRYGER leg., 3 ♂♂ reared about 8. VI. 1914 from same sample, Coll. LUNDBECK, (ZMC).

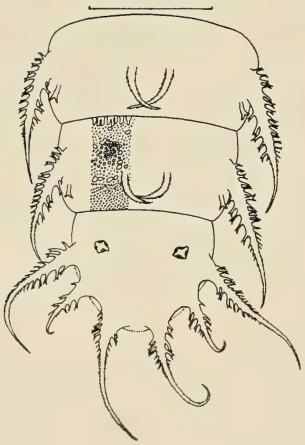
Denmark, Zealand, Dyrehaven, 2 puparia collected in nest of *Vespa* sp., 1 ♂ 1 ♀ reared 17. VI. 1912, Coll. LUNBDECK, (ZMC).

Description. Very similar to the larva of *fuscula* described above and compared with *fuscula* in the following diagnosis.

Dorsal view. Anterior processes of segment 1 shorter than in *fuscula*. Prothoracic spiracles with 9 processes. Laterodorsals of segments 2—10 shaped as in *fuscula*, but lateral projections shorter and of more gradually decreasing size towards the apices. Dorsolaterals with longer stems than in *fuscula*. Dorsomedians of segments 2—10 shorter than in *fuscula* and without long, lateral projections. No projections anterior to base of dorsomedians. — Terminal segment almost identical with that of *fuscula*, though marginal processes shorter and with shorter basal projections. — Posterior spiracles and integument as in *fuscula*.

Ventral view. Lateroventrals as in *fuscula*, but shorter and weaker, and those of segment 2 not much larger than four small prominences present on line between lateroventrals. These four prominences (ventrolaterals and ventromedians) also present on segment 3. Ventrolaterals also developed on segments 4—11, where they are about half as long as in *fuscula*. Four small prominences as found on posterior part of segments 4—10 in *fuscula* not developed in *vesparia*, though short, transverse ridges with same arrangement can be seen on segments 4—5 or 4—6. Segments 5—10 not distinctly divided into two parts by transverse furrows.

Length of puparium: about 8 mm.



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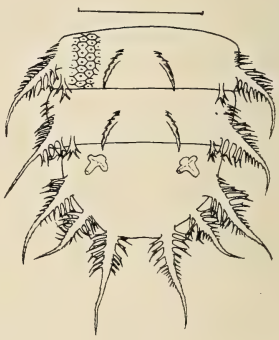

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Fig. 9. Segments 9—11 in dorsal view of larva of *Fannia vesparia* Meade. Scale: 1 mm.
Fig. 10: Segments 9—11 in dorsal view of larva of *Fannia leucosticta* Meig. Scale: 1 mm.

Fannia leucosticta Meigen, 1826. (Fig. 10).

Material: N. Rhodesia, Mazabuka, 23. II. 1932, 1 puparium ex dead unparasitised *Nomadacris septemfasciata*, 1 ♂ reared, (BM).

Description.

Dorsal view. Segment 1 with short and slender anterior processes; no lateral processes. Anterior spiracles with about 7 processes. — Segments 2—10 with laterodorsals longer than length of corresponding segment, at least on the last segments. — Laterodorsals of segment 2 with only short projections, those of following segments have some rather long, bifurcate projections in basal parts. Projections of apical parts gradually shorter, minute on apices. — Dorsolaterals of segments 2 and 3 developed as small prominences with few short projections and situated on anterior parts of these segments at a good distance from lateral margins. Same processes of segments 4—10 longer, with few long projections and situated close to base of laterodorsals. Dorsomedians of segments 2—10 of gradually increasing length towards the caudal segments, those of segments 9—10 nearly as long as a segment, and all bear spinelike projections, especially on anterior surfaces. — Sublateral pair of terminal processes shorter than other two pairs. All terminal processes with projections as described for laterodorsals. — Posterior spiracles on long stalks placed on dorsal surface of segment at a good distance from lateral margin. Median spiracular process longest and directed upwards and outwards. — Integument with a polygonal pattern.

Ventral view. Segment 2 with three pairs of small prominences, namely a pair representing lateroventrals close to base of laterodorsals, further a median pair representing ventromedians and finally an intermediate pair with more posterior position and representing ventrolaterals. — Lateroventrals of segment 3 about half as long as segment, those of following segments gradually longer, all provided with simple projections. — Ventrolaterals and ventromedians of segments 3—10 developed as button-like prominences placed on a line near anterior margin of segment 3, while ventromedians are near posterior margins and ventrolaterals about midway between anterior and posterior margins on the following segments.

Length of puparium: 4.5 mm.

Fannia canicularis Linné, 1761. (Figs. 1 f, 11).

Material:

Denmark, Zealand, København, 15 larvae and puparia collected 1. XI. 1907 in decaying cucumber, some imagines reared shortly after, Coll. LUNDBECK, (ZMC).

Same locality, 34 larvae and puparia collected in decaying apples 12. VII. 1916, 1 ♂, 2 ♀♀ reared 1. — 10. X. 1916, Coll. LUNDBECK, (ZMC).

Same locality, 27 puparia collected from decaying insects, 6 ♂♂, 5 ♀♀ reared, Coll. LUNDBECK, (ZMC).

Same locality, 19 larvae and puparia collected in nest of *Bombus*, 2 ♀♀ reared, (ZMC).

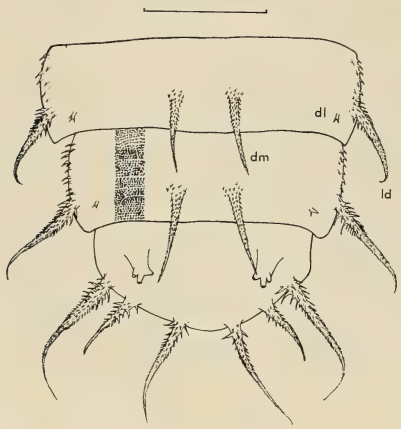
Description.

Dorsal view. Segment 1 with moderately long, anterior processes; no lateral processes. Prothoracic spiracles with about 8 processes. — Segments 2—10 with long and slender laterodorsals provided with short and simple lateral projections. — Segments 2—10 with dorsolaterals on segment 2 developed as short and simple processes situated at anterior margin midway between dorsomedians and laterodorsals; on the following segments developed as short, bifurcate or trifurcate projections situated midway between dorsomedians and laterodorsals on segment 3 and medially to base of laterodorsals on the following segments. — Dorsomedians of segments 2—10 long, slender, and of increasing length towards the caudal segments. They are provided with short projections which are also found anterior to base of processes. —

Terminal segment with six long and slender processes; sublateral pair shortest and nearer to lateral than to subapical pair. All processes have lateral projections as described for the laterodorsals. — Posterior spiracles on long stalks placed nearer to lateral margin than to midline. The two lateral spiracular processes placed close together. — Integument densely granulated, elements forming a more or less distinct, reticulate pattern, divided up by depressed lines.

Ventral view. Segments 2—10 with lateroventrals which are very short on segment 2, thrice as long on segment 3, and on following segments more than half as long as a segment. They are provided with short projections. — Ventrolaterals developed as prominences with short, spinelike projections on segments 2—11. — Ventromedians developed on segments 4—10 as four prominences similar to, but smaller than, ventrolaterals just described, situated on posterior half of each segment (compare fig. 2). More laterally (just behind the ventrolateral prominences) with an additional group of short, spinelike projections.

Length of puparium: about 6 mm.



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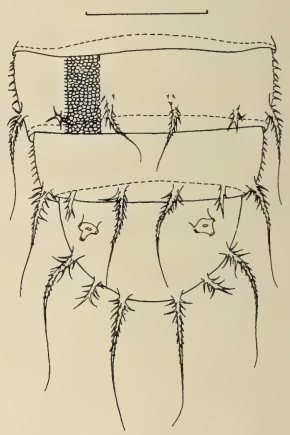

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Fig. 11. Segments 9—11 in dorsal view of larva of *Fannia canicularis* L. Scale: 1 mm. Abbreviations: dl = dorsolaterals, dm = dorsomedians, ld = laterodorsals.
Fig. 12. Segments 9—11 in dorsal view of larva of *Fannia clara* Coll. Scale: 1 mm.

Fannia aequilineata Ringdahl, 1945.

Material: Great Britain, Oxford, University Parks, 3 puparia, collected in January-February 1926 as larvae in old Blackbird's nest, 2 ♂♂, 1 ♀ reared 16. IV.—8. V. 1926, A. H. Hamm, (Oxf. Mus.).

Description.

Unfortunately most processes are broken in the three puparia available, for which reason a precise description is impossible. It can be stated that the larva of *aequilineata* is very similar to the larva of *canicularis*. The following differences were noted: lateral projections of laterodorsals as well as of dorsomedians longer and often slighty bifurcate. Dorsolaterals short as in *canicularis*, but with some much longer basal projections.

Length of puparium: about 6.5 mm.

Fannia clara Collin, 1939. (Fig. 12).

Material: Great Britain, Bucks., Greenlands, 17. VII. 1936, 1 puparium attached to male specimen reared from nest of Heron (No. H. 2), (BM).

Description.

Dorsal view. Anterior processes of segment 1 broken in the single specimen available; no lateral processes. Prothoracic spiracles with 8 processes. — Segments 2—10 with very slender laterodorsals of about same length as corresponding segments. They are provided with rather few and not very long, simple, lateral projections at base. The longest of these projections are longer than basal width of laterodorsals. Apical parts of laterodorsals thread-like and with very minute projections. — Segments 2—10 with dorsolaterals; on segment 2 developed as short and simple, thread-like processes situated near anterior margin and mid-way between dorsomedians and laterodorsals, on the following segments provided with some long projections and placed at a good distance from base of laterodorsals. — Dorsomedians of segments 2—10 similar to laterodorsals, though shorter. Row of short, spinelike projections present on dorsolateral margin of segments. — Sublateral pair of terminal processes much shorter than lateral and subapical pairs. All processes provided with simple projections which gradually decrease in length towards the threadlike apices. — Posterior spiracles on rather long stalks placed nearly mid-way between midline and lateral margin. Spiracular processes arranged with equal distances. — Integument evenly and rather coarsely granulated.

Ventral view. Segments 2—10 with lateroventrals which are short and simple on segment 2 (about one-eighth of the total length of segment), four times longer on segment 3 and of segmental length on the rest. They are provided with projections similar to projections of laterodorsals. Row of short spinelike projections on ventrolateral margin. — Segments 2—11 with ventrolaterals shaped as small prominences on segment 2 and as groups of short projections on segment 3. On the following segments they appear as short processes provided with short projections. — Ventromedians developed on segments 2—3 as two groups of short projections medially to the two groups representing the ventrolaterals. Transverse rows of short, spinelike projections including a pair of bifurcate projections situated on posterior part of segments 4—10 and represent ventromedians of these segments. Similar transverse rows of smaller spinelike projections present on anterior parts of segments 5—10 on a line connecting ventrolaterals. — Segments 5—10, as indicated above, divided into two parts by transverse furrows.

Length of puparium: about 6 mm.

Fannia vespertilionis Ringdahl, 1934. (Figs. 1 g, 13, 14).

Material:

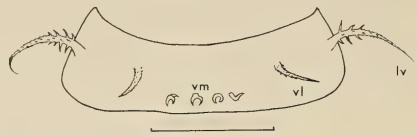
Denmark, Zealand, København, 9 larvae (of very different size) and puparia collected 25. IX. 1915 in nest of *Sturnus vulgaris*, J. P. Kryger leg., 2 ♂♂ reared 18. V. 1916, Coll. Lundbeck, (ZMC).

Denmark, Zealand, Frederikslund, 7 puparia collected 9. X. 1910 in nest of *Sturnus vulgaris*, E. Suenson leg., 3 ♂♂, 3 ♀♀ reared 11. III. to 6. IV. 1911, Coll. Lundbeck, (ZMC).

Description. The larva of this species is very distinct from all other known *Fannia* larvae because of its almost cylindrical shape and the six long and nearly equal, dorsal processes.

Dorsal view. Segment 1 with long, slender anterior processes; no lateral processes. Prothoracic spiracles with 8 processes. — Segments 2—10 with three pairs of nearly equal processes: dorsomedians, dorsolaterals and laterodorsals. Dorsolaterals about as long as the other two pairs of processes on the first segments, while they are distinctly shorter on the last segments. Distances between the six

processes are almost the same on segments 2, 3 and 10, while the dorsolaterals are distinctly nearer to laterodorsals than to dorsomedians. All processes slender and provided with only a few and short, scaly, lateral projections. — Terminal segment with two very long, subapical processes. Sublateral processes much shorter and lateral processes nearly as long as subapicals, but inserted more dorsally. All six terminal processes with only short and few, lateral projections. — Posterior spiracles on distinct stalks placed mid-way between midline and lateral margin. Three long spiracular processes present; two of them arranged close together laterally; the third directed inwards and backwards. — Integument densely granulated.



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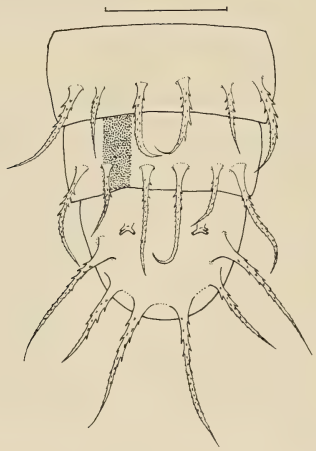

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Fig. 13. Segment 4 in ventral view of larva of *Fannia vespertilionis* Ringd. Scale: 1 mm. Abbreviations: lv = lateroventrals, vl = ventrolaterals, vm = ventromedians.

Fig. 14. Segments 9—11 in dorsal view of larva of *Fannia vespertilionis* Ringd. Scale: 1 mm.

Ventral view. Segments 2—10 with lateroventrals which are short and slender on segment 2; only one-sixth the length of laterodorsals of same segment. They are about half as long as laterodorsals on segment 3, and on the following segments of nearly same length as laterodorsals. Ventrolaterals of segments 3—11 relatively long, though always distinctly weaker than lateroventrals of same segment. — Segment 3 with a pair of small, button-like prominences representing the ventromedians on a line between ventrolaterals (as in fig. 2). — Segments 5—10 divided into two parts. The above mentioned ventrolaterals placed on a ridge on anterior part of each segment, while ventromedians of segments 4—10 are represented by four prominences at posterior margins. They have a very characteristic shape, as they are deeply cleft and thus U-shaped. Additional prominences sometimes present more laterally. They may be of the shape just described or entirely divided up into two simple, spinelike projections.

Length of puparium: about 7 mm.

Fannia lineata Stein, 1895. (Figs. 1h, 15).

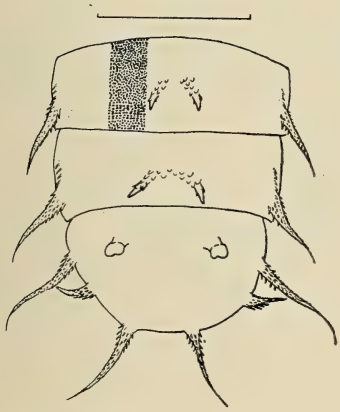
Material: Denmark, Zealand, København, 1 larva and 1 puparium collected 25. IX. 1915 in nest of *Sturnus vulgaris*, J. P. KRYGER leg., 1 ♀ reared 18. V. 1916, Coll. LUNDBECK, (ZMC).

Description.

Dorsal view. Segment 1 with rather long and thin anterior processes; without lateral processes. Prothoracic spiracles with 3 processes. — Segments 2—10 with rather short and slender laterodorsals, provided with only short and simple lateral projections. — Dorsolaterals not developed. — Dorsomedians short and present on segments 2—10. Anterior to base of dorsomedians are some short, blunt projections, arranged more or less in a bow. Lateral and subapical processes of terminal segment of nearly equal size, while sublaterals are much shorter, placed nearer to lateral than to subapical processes and curved towards the rear. All six processes have short and simple lateral projections. — Posterior spiracles on short stalks mid-way between lateral margin and midline. — Integument granulated.

Ventral view. Segments not divided by transverse furrows. Segments 2—10 with simple, lateroventral processes. These very short on segment 2; on the following segments about two-fifths as long as a segment. — Ventrolaterals present on segments 4—11 as small, button-like prominences. — No traces of ventromedians.

Length of puparium: 5.5 mm.



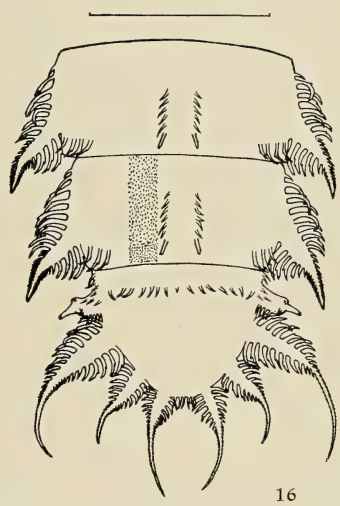


Fig. 15. Segments 9—11 in dorsal view of larva of *Fannia lineata* Stein. Scale: 1 mm.
Fig. 16. Segments 9—11 in dorsal view of larva of *Fannia umbrosa* Stein. Scale: 1 mm.

Fannia umbrosa Stein 1895. (Figs. 1i, 16).

Material:

Denmark, Zealand, Rådvad, 6 puparia collected 9. IV. 1916 in rotten oakwood, J. P. KRYGER leg., 1 ♂, 1 ♀ reared, Coll. LUNDBECK, (ZMC).

Denmark, Zealand, Asserbo, 2 puparia collected 19. V. 1917 in nest of *Sturnus vulgaris*, 1 ♂ reared June 1917, Coll. LUNDBECK, (ZMC).

Denmark, Zealand, Hareskov, 6 puparia collected 23. III. 1910 in sap of beech-stump, J. P. KRYGER leg., 5 ♂♂, 1 ♀ reared 2.—8. V. 1910, Coll. LUNDBECK, (ZMC).

Denmark, Zealand, Ermelund, 1 larva and 1 puparium collected 19. III. 1911 in rotten oak-stump, J. P. KRYGER leg., 1 ♀ reared 27. IV. 1911, Coll. LUNDBECK, (ZMC).

Denmark, Zealand, Bøndernes Hegn, 1 larva collected 3. II. 1962 under bark of ash-tree, O. MARTIN leg., (ZMC).

Description.

Dorsal view. Segment 1 with long, slender, anterior processes, and a pair of much shorter, lateral processes. Anterior spiracles with 4 processes. — Segments 2—10 with rather short laterodorsals which are broad at base. They are provided with long, bifurcate, lateral projections in basal parts, except on segment 2 where they are absent. On segment 3 the projections are found on posterior part only. These lateral projections continue on lateral margin of the segments to near anterior margin on the caudal segments. Apical parts of laterodorsals short and densely covered with much shorter projections. — Dorsolaterals represented on segments 2 and 3 by simple processes similar to lateral processes of segment 1 and placed near anterior corners of these two segments. Dorsolaterals of segments 4—10 developed as 2—4 projections near posterior margin and medially to base of laterodorsals, thus forming a continuation of the projections on posterior part of these processes. — Segments 2—10 with short, but distinct, dorsomedians placed near anterior margins on segments 2 and 3 and near posterior margins on the following segments. — A row of spinelike projections anterior to base of dorsomedians of segment 5—10. One similar projection may be present on segment 4. — Terminal segment with a transverse row of rather short, spinelike projections near anterior margin. Subapical processes slightly longer than sublateral processes. Lateral processes longest and strongest. Apical parts of all six terminal processes longer and more slender than those of the laterodorsals of normal segments. — Posterior spiracles on stout stalks inserted on lateral margin anterior to base of lateral processes. One of the spiracular processes long, the other two short and arranged around base of long process. — Integument sparsely granulated.

Ventral view. Segments 5—10 divided into two parts by transverse furrows. Segments 2—10 with lateroventral processes which are very short on segment 2 and on the following segments about one-fourth of the length of the segments. Small ventrolaterals at anterior margin of segments 2 and 3. Still smaller and more widely separated ventrolateral prominences on segments 4—11. Ventromedians not visible. Integument of segments 1—3 forming polygonal pattern; on the following segments more granulated.

Length of puparium: about 5 mm.

Fannia armata Meigen, 1826. (Fig. 17).

Material: Denmark, Zealand, Dyrehaven, 1 puparium collected 13. IV. 1914 on beech-stump, J. P. Kryger leg., 1 ♂ reared 10. V. 1914, Coll. Lundbeck, (ZMC).

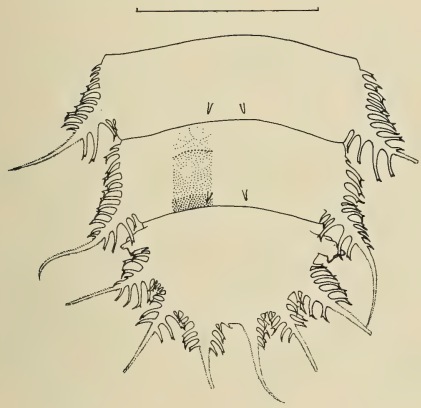
Description.

Dorsal view. Segment 1 with long, slender, anterior processes; and much shorter lateral processes (as in fig. 1 i, but shorter and placed nearer anterior corners). Prothoracic spiracles with 4 processes. — Segments 2—10 with long, laterodorsals provided with long, lateral projections in basal parts. These projections often bifurcate and developed to near anterior margin of each segment. Apical parts of laterodorsals long, slender and with very short projections. — Dorsolaterals seem only developed on segment 2, situated near anterior margin, long and slender, i. e., half as long as the segment (compare fig. 1 i of *umbrosa*, where they are distinctly shorter). In *umbrosa* similar dorsolaterals also on segment 3, but these are absent in *armata*. Also segments 4—10 without dorsolaterals. — Segments 2—10 with very short dorsomedians placed near anterior margins on segments 2 and 3 and near posterior

margins on the following segments. — Terminal segment with six nearly equal processes which have long, lateral projections in basal parts and very short projections in apical parts. — Posterior spiracles on stout stalks on lateral margin anterior to base of lateral processes. Two long and one short spiracular processes. One long process directed upwards and one long outwards, while the short one is situated anteroventrad to base of the long processes. — Integument granulated; its elements often forming a polygonal pattern, especially on anterior part of each segment.

Ventral view. Segments 5—10 divided into two parts by transverse furrows. Segments 2—10 with short lateroventrals. Their length about one-fourth the length of a segment and of nearly equal size on all segments. They are provided with only very short projections. Segments 2 and 3 with two pairs of small prominences on a line between lateroventrals. Lateral pair represents ventrolaterals which are found as small prominences also on anterior parts of the following eight segments. Median pair represents ventromedians, which are found as two widely separated prominences on posterior parts of segments 4—10.

Length of puparium: 5.5 mm.



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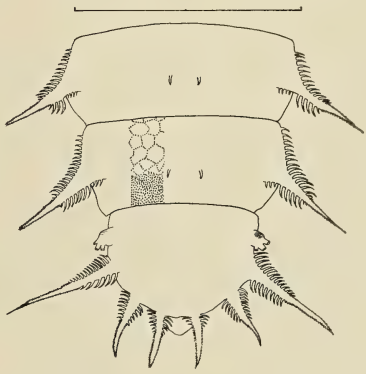

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Fig. 17. Segments 9—11 in dorsal view of larva of *Fannia armata* Meig. Scale: 1 mm.
Fig. 18. Segments 9—11 in dorsal view of larva of *Fannia ?tuberculata* Zett. Scale: 1 mm.

Fannia ?tuberculata Zetterstedt, 1849. (Fig. 18).

Material: Iceland, Bæjarstadaskogur, 2 larvae collected August 1932, G. Gigja leg., (ZMC).

Description.

Dorsal view. Segment 1 with long and comparatively strong anterior processes. Same segment with lateral processes which are about one-third as long as anterior processes. Prothoracic spiracles with 5 processes. — Segments 2—10 with relatively long and slender laterodorsals. Laterodorsals of segment 2 with very short lateral projections, but the laterodorsals of segment 3 with a few, rather long, lateral projections on posterior part. Laterodorsals of the following segments provided with rather long, lateral projections on both anterior and posterior parts. Apical parts with very short projections. Projections of anterior parts continue to near anterior margin of segments. Projections of posterior parts continue as smaller projections on a short ridge medially to base; these projections represent dorsolaterals. Dorsolaterals distinctly developed on segments 2 and 3, where they appear as short and simple processes situated at base of much stronger laterodorsals. — Dorsomedians

extremely small and present on segments 2—10. — Terminal segment with subapical and sublateral processes rather short and of nearly equal size, while lateral processes are nearly twice as long. All six processes bear rather long, lateral projections in basal parts and very short projections in apical parts. — Posterior spiracles on short stalks on lateral margin anterior to lateral processes. Three almost equal spiracular processes. — Integument forming polygonal pattern on anterior parts, and densely granulated on posterior parts of segments.

Ventral view. Segment 5—10 divided into two parts by transverse furrows. Segments 2—10 with lateroventrals. These very short on segments 2 and 3, while they are about one-fourth as long as a segment on the following segments. — Ventrolaterals present as small, button-like prominences on segments 2—11. — Ventromedians not developed.

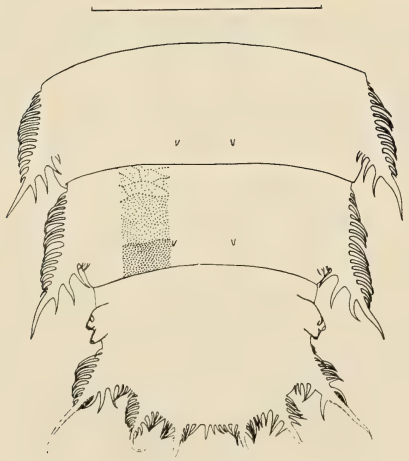
Length of larva: 5.5 mm.

Fannia genualis Stein, 1895. (Figs. 1j, 19).

Material: Denmark, Zealand, Sorø Sø, 1 larva and 1 puparium collected 15. IV. 1904 in flood refuse, 1 ♂ reared 2. V. 1904, Coll. LUNDBECK, (ZMC).

Description.

Dorsal view. Segment 1 with long, slender, anterior processes. Lateral processes extremely small, shorter than spiracular processes. Prothoracic spiracles with 7 processes. — Segments 2—10 with rather short laterodorsals. Anterior projections of these processes numerous, simple and developed to near anterior margins of segments. Posterior projections longer but fewer (about three). Laterodorsals of segment 2 and also anterior parts of laterodorsals of segment 3 with very short projections. — Dorsolaterals not developed, though a few short projections medially to base of laterodorsals of segments 9—10 may represent these structures. — Dorsomedians very short and present on segments 2—10. — Terminal processes short and of decreasing size from lateral pair to subapical pair. All processes have simple projections at base. — Posterior spiracles on short stalks anterior to lateral processes and a little dorsad to lateral margin. Posterior spiracular processes longest. —



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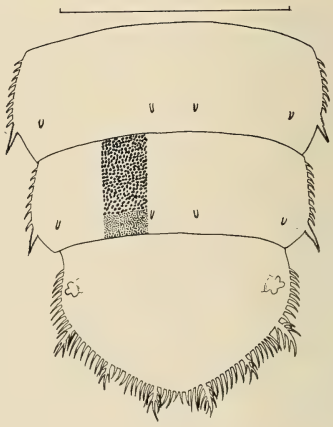

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Fig. 19. Segments 9—11 in dorsal view of larva of *Fannia genualis* Stein. Scale: 1 mm.
Fig. 20. Segments 9—11 in dorsal view of larva of *Fannia mollissima* Hal. Scale: 1 mm.

Integument densely granulated; its elements forming lines of a polygonal pattern in anterior parts of segments.

Ventral view. Segments 5—10 divided into two parts by transverse furrows. Segments 2—10 have simple lateroventrals which are very short on segments 2 and 3, longer on the following segments, i. e., about one-sixth the length of a segment. Two pairs of small, button-like prominences present on line between lateroventrals of segments 2—3, lateral pair representing ventrolaterals, which are also present as small prominences on anterior parts of segments 4—11. Median pair represents ventromedians which are also present as four prominences on posterior parts of segments 4—10.

Length of puparium: 4.5 mm.

Fannia mollissima Haliday, 1840. (Figs. 1 k, 20).

Material:

Iceland, Kirkjubæjarklaustur, 1 larva collected in August 1932, G. Gigja leg., (ZMC).
Faroes, Myggenæs, 1 larva collected 12. IX. 1926 under stone, H. Lemche leg., (ZMC).
Faroes, Strömö, St. 32, 4 larvae collected 2. X. 1925, H. Lemche leg., (ZMC).
Faroes, Kirkebö, St. 10, 1 larva collected 9. IX. 1925 in stone-fence, H. Lemche leg., (ZMC).
Faroes, Thorshavn, 4 larvae collected 20. IV. 1925 under bark, J. P. Kryger leg., (ZMC).
Faroes, Thorshavn, 20 larvae collected 7. IX. 1925 in hay on field, H. Lemche leg., (ZMC).

Description.

Dorsal view. Segment 1 with rather long, slender, anterior processes, and very short lateral processes anterior to prothoracic spiracles. These have about 12 processes. — Segments 2—10 with very short laterodorsals. Their length about one-fourth of length of a segment, and they are provided with very short projections. Lateral margins anterior to laterodorsals with row of short spinelike projections. — Segments 2—10 with extremely small and simple dorsolaterals about the same size as laterodorsals of preceding segments, but provided with long, slender lateral projections. Also margin of terminal segment with long, slender and simple projections. — Posterior spiracles on short stalks situated on dorsal side near lateral margin. Three spiracular processes of equal size. — Integument granulated, most finely and densely on posterior part of each segment.

Ventral view. Segments 4—10 divided into two parts by transverse furrows. — All three pairs of ventral structures very small. On segments 2 and 3 are six groups of short, spinelike projections, situated on a line on anterior parts of segments. Lateral pair of these groups represents lateroventrals which are present also on segment 4—10 as small, button-like prominences. Intermediate pair represents ventrolaterals which are present as small prominences also on segments 4—11 and here situated at the ends of ridges on anterior halfs of the segments. The ridges have row of short, close-set, spinelike projections. On posterior parts of segments 4—10 are four groups of short, spinelike projections; these groups represent the ventromedians.

Length of larva: about 5.5 mm.

VI. Summary

Descriptions and figures are given of the external morphology of the larvae of eighteen European species of *Fannia* R.-D. Eight of these larvae were unknown and some of the remaining ten larvae have been only imperfectly described by earlier

authors. A key to the eighteen larvae is presented. Furthermore, a section on the comparative, external morphology of *Fannia* larvae is presented on the basis of these eighteen descriptions. Finally, there is a short discussion of the larval morphology as evidence for the phylogenetic value and relationships of the species groups established by CHILLCOTT (1961).

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